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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA V. A NEW CHINIQUODONTID CYNODONT, *PROBELESODON LEWISI* — CYNODONT ANCESTRY

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ABSTRACT. A carnivorous cynodont from the Middle Triassic Chañares fauna of Argentina is described as *Probelesodon lewisi*, gen. et sp. nov. This is an advanced cynodont with an elongate mammal like secondary palate, related to the chiniquodontids of the Santa Maria Formation of Brazil. The short face and recurved molars indicate descent from thrinaxodontids rather than the Cynognathidae. Cynodont ancestry is discussed. There is no evidence of derivation from scaloposauroids and presumably the cynodonts are of independent descent from the ancestral theriodonts.

INTRODUCTION

As is generally recognized, a marked change took place during the Triassic in the nature of the terrestrial predaceous vertebrate fauna. In the early Triassic Karroo beds carnivorous therapsids are dominant; in the late Triassic, therapsids (except those which have progressed to the mammalian stage) are practically extinct, and archosaurs — thecodonts, crocodilians, dinosaurs — have replaced them as the major carnivores. Until recently, Middle Triassic terrestrial vertebrate faunas were almost unknown, but it would be expected that, at that time, there would have been transitional conditions, in which predaceous therapsids would be undergoing reduction, and archosaurs, on the other hand, would be increasing in abundance and diversification.

Our currently increasing knowledge of the excellent series of Middle Triassic beds of South America shows that this is indeed the case. The faunas of this age now known from that continent form a sequence including, in descending order, assemblages present in these three formations: Ischigualasto (Argentina), Santa

Maria (Brazil), and Chañares (Argentina). In these beds, predaceous cynodonts are undergoing sharp reduction. In the uppermost of the three faunas, that of Ischigualasto, only a single fragmentary specimen of a carnivorous cynodont has so far been recovered (Bonaparte, 1966). In the extensive collections made by Huene (1944) in the Santa Maria beds, there were but two carnivorous cynodonts, each represented by a single specimen; further collections made for Harvard and the American Museum included only a very few additional individuals. But when we descend to the lowest of the three faunas, that of the Chañares Formation, we find that cynodont reduction is relatively less marked. Only two predaceous members of that group are present, but they are moderately abundant. Our collections include more than a score of specimens.

The present work is limited to a description of the cranial anatomy of the larger of the two forms present. I plan shortly to publish on the cranium of the second cynodont, and later, on postcranial materials of both forms.

The cynodont here described may be formally named and characterized as follows:

PROBELESODON LEWISI gen. et sp. nov.

Combined generic and specific diagnosis. A chiniquodontid cynodont, closely related to *Belesodon* and *Chiniquodon*, but of smaller size than the former, the more mature individuals reaching an average skull length, from snout to condyles, of about 140 mm; the secondary palate long; generally with nine maxillary cheek teeth, the "molars" multicuspidate, the main cusp backwardly curved.

Holotype of the species. No. 64-XI-14-6, La Plata Museum, a skull and jaws collected from the Chañares Formation in La Rioja Province, Argentina, about 10 km east of the point where the Río Chañares emerges into the Plano de Talampaya.

The generic name is due to the obviously close relationship, discussed later, of this form, to *Belesodon* (and *Chiniquodon*) of the somewhat later Santa Maria beds; the specific name is given in honor of Arnold D. Lewis, chief preparator at the Museum of Comparative Zoology, who played a major part in the collection of the Chañares material.

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THE SKULL

(Figs. 1-5)

Of *Probelesodon*, nine skulls have so far been discovered. Of these, five representing apparently mature individuals are members of a single size group, with lengths from premaxillae to condyles in four of them measuring: 143, 137, 132, and 130 mm (a fifth member of this group is incomplete posteriorly). A skull which is incomplete in the occipital region is obviously larger and probably measured about 155 mm in length. The holotype, on the other hand, is somewhat smaller, with a basicranial length of 115 mm. It is probably somewhat immature; it may be noted that a replacement of canines is taking place. Two "juveniles" have been found. One measures 72 mm in length; the second lacks the occiput but was of approximately the same size.

In general proportions, the skull resembles certain of the *thrinaxodontids* and differs from such well known forms as *Cynognathus* and *Diademodon* in its relatively short muzzle and broadly flaring zygomatic arches, the width across the arches reaching 75 to 80 per cent or more of skull length. Anterior to the external nares the skull terminates in a pointed snout. In cross section the muzzle is rounded, curving inward ventrally somewhat toward the tooth rows of the cheeks, although this ventral curvature is not so great as in, for example, the contemporary *gomphodonts*. In advanced fashion the sagittal crest is high and thin, as are the occipital crests. The zygomatic arches are moderately deep, but the arch and occipital crest connect only by a narrow waist, in contrast to the broad sweep of the squamosal connecting the two in many other cynodonts. The postorbital arch is narrow. The orbits are situated close to the half length of the skull. The parietal foramen appears to be generally absent; if perhaps present in some specimens, it is at best vestigial. As in other advanced cynodonts, the occipital condyle is definitely double. Most notable of distinctive characters is the great development of the secondary palate, unmatched in any other known cynodonts except the related *chiniquodontids* of Santa Maria.

In external exposure the premaxillae form the area of origin of the four incisors on either side, and the ventral and medial borders of the external nares. Conjoined processes of the two premaxillae extend upward and forward anterior to the nares to form the pointed snout tip and then, diminishing gradually in size, turn backward above as slender rods separating the nasals for a considerable distance. A septomaxilla is present, presumably of the

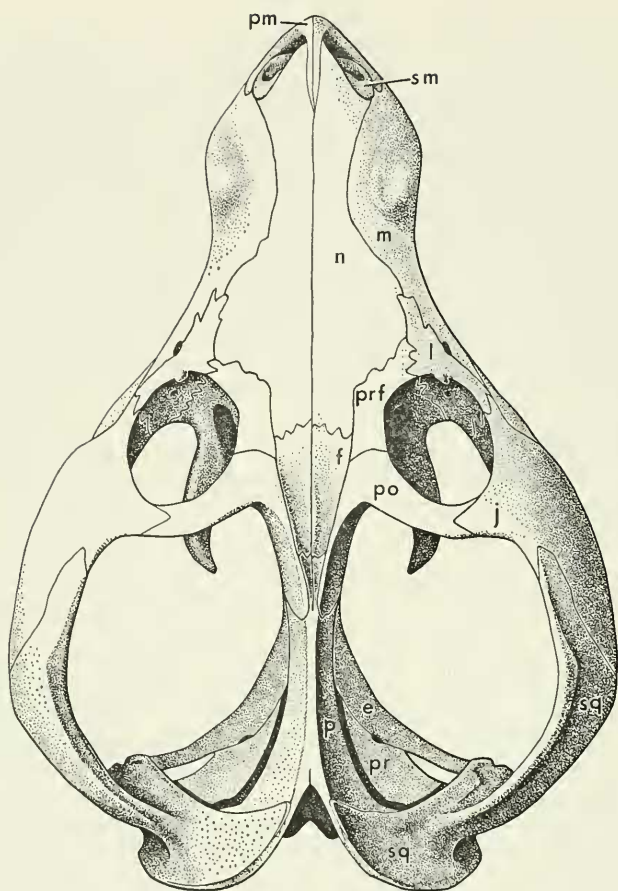


Fig. 1. *Probelesodon lewisi*, dorsal view of skull. This and the following figures of the skull and jaws are based primarily on the type, with supplementary data from other specimens. Figures 1-7 are the size of the type and approximately $\frac{3}{4}$ times the size of the largest mature specimens. Abbreviations for Figures 1-7: *a*, articular; *an*, angular; *bo*, basioccipital; *bs*, basisphenoid + parasphenoid; *d*, dentary; *e*, epipterygoid; *ec*, ectopterygoid; *f*, frontal; *fo*, fenestra ovalis; *j*, jugal; *jf*, jugular foramen; *l*, lacrimal; *m*, maxilla; *n*, nasal; *oc*, occipital complex; *p*, parietal; *pap*, paroccipital process; *pl*, palatine; *pm*, premaxilla; *po*, postorbital; *pp*, postparietal; *ppf*, pterygo-paroccipital foramen; *pr*, prootic; *pra*, prearticular; *prf*, prefrontal; *pt*, pterygoid; *ptf*, posttemporal fenestra; *q*, quadrate + quadratojugal; *sa*, surangular; *sm*, septomaxilla; *sp*, splenial; *sq*, squamosal; *t*, tabular; *v*, vomer; *v₂* + *a*, foramen for trigeminal nerve; *vg*, groove for a vein.

typical cynodont type, but was apparently loosely articulated, is frequently absent in the specimens and is never well preserved. The maxilla is a large element, extending from the narial region back along the side of the snout and, curving outward, has a somewhat thickened terminus, below the orbit, which projects notably below the level of the jugal arch. This contrasts with the pattern seen in such cynodonts as *Cynognathus* and *Diademodon*, in which a suborbital projection is formed by the jugal rather than the maxilla. Behind the naris, the maxilla, in relation to the obviously deep root of the canine, extends, in contact with the nasal, far up the snout toward the midline; posterior to the canine region, its margin turns downward again, bordered posteriorly by the lacrimal and jugal, to terminate at the ventral process mentioned above. Several small foramina penetrate the maxilla, and an especially large one is present between the maxilla and the lower border of the lacrimal. The region containing the canine root is prominently swollen, and the face is expanded ventrally at the region of the emergence of the canine. The canine swelling is especially prominent in the larger specimens, and there tends to develop a clearly marked channel curving around the base of the canine root.

Of the median roofing elements, the nasals, as in cynodonts generally, are very long; here they reach back half the length of the skull roof to terminate between the orbits. They form the upper margins of the nares; continuing backward between the maxillae, they are somewhat constricted in width in the region of the canine roots. They expand laterally to bound the dorsal margins of the lacrimals, and then constrict again between the prefrontals to a nearly directly transverse suture with the frontals. Since this suture is considerably farther posterior than is common in therapsids, the frontals are reduced in length and area, and are essentially a pair of triangular wedges, separated suturally from the postorbitals between and below backwardly converging ridges. The frontals appear to be exposed laterally within the orbital rim, between prefrontals and postorbitals. The parietals have as a main function the formation of a high median sagittal crest. For most of their length, the two are solidly fused at the narrow tip of the crest. Anteriorly, they diverge slightly for a short distance. The parietals descend some distance down the gradually diverging sides of the sagittal crest, overlapped anteriorly by the postorbitals. Posterior to the postorbitals the lower margins of the parietals extend backward along the line of the vein whose course can be often followed in cynodonts, bounded below by the epipterygoid

and the prootic region of the braincase. In contrast to conditions in some other cynodonts, the venous channel and the parietal-epipterygoid boundary seem to coincide. There is visible here, in some specimens, an unossified area, presumably cartilage-filled in life, between parietal above and prootic below. As in cynodonts generally, the two parietals diverge posteriorly to take part in the formation of the occipital crests.

Of the series of circumorbital elements, the lacrimal occupies much of the anterior margin of the orbital rim and extends forward and upward as in cynodonts generally, to gain a contact with the nasal as well as having the normal external contacts with the prefrontal dorsally, maxilla anteroventrally, and jugal posteriorly at the lower orbital margin. The bone also forms a portion of the ossified anterior surface of the orbital socket, between prefrontal above and jugal below. Ventrally in the orbit, the lacrimal has a firm connection with the dorsal surface of the palatine. On the orbital rim, external to the lacrimal foramen, there tends to develop an osseous protuberance, most prominent in the large specimens, the function of which is uncertain. The jugal is, as usual, highly developed. Dorsally, it forms part of the relatively narrow postorbital bar; anteriorly, it extends forward below the orbit to meet the maxilla and lacrimal and internally forms the most ventral part of the orbital wall. Anterointernally, it gains a contact with the ectopterygoid and pterygoid at the lateral margin of the palatal plate. As noted above, there is no development of a suborbital process of the sort seen in *Cynognathus*, *Diademodon*, etc. The main ramus of the jugal extends posteriorly to form a great part of the substance of the deep zygomatic arch. It reaches posteriorly and ventrally nearly to the posterior root of the arch, although sheathed externally over most of its course by the squamosal. The postorbital forms the upper part of the postorbital bar, and extends somewhat anteriorly and medially on the skull roof. Posteriorly on the roof, a pair of flanges from the postorbitals, ridged on their medial margins, extend backward from the prefrontals, constricting the frontals between them. Below these dorsal processes, the postorbitals extend backward on either side of the base of the sagittal crest for some distance, sheathing the parietals externally. The prefrontal has a modest external exposure along the upper orbital margin, bounded medially by the nasal and frontal, anterolaterally by the lacrimal, posteriorly by the postorbital. Internally, it continues upward the orbital wall formed more ventrally by lacrimal and jugal and dorsomedially by the frontal.

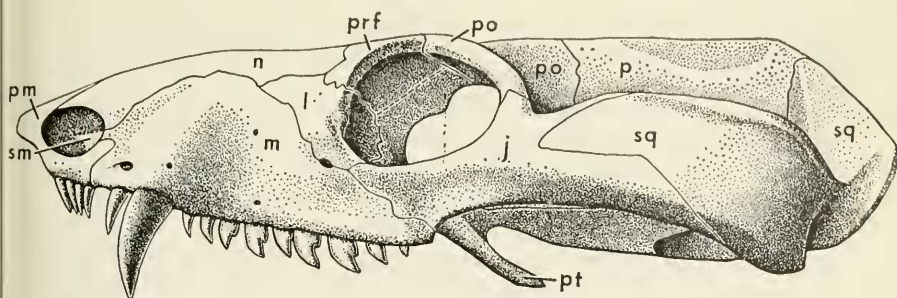


Fig. 2. Lateral view of the skull of *Probelesodon lewisi*.

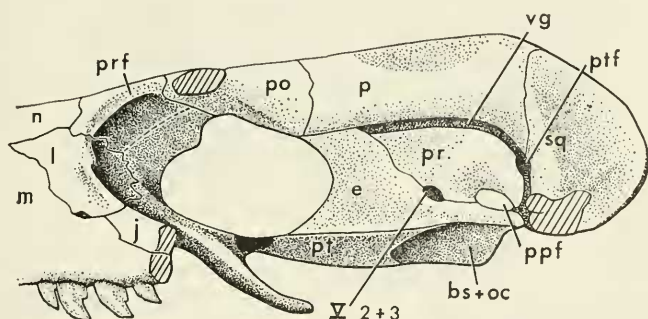


Fig. 3. Lateral view of the skull of *Probelesodon lewisi*, with the zygomatic arch removed.

The squamosal is one of the largest as well as the most complex of cranial elements. It consists of two major rami, the two connected by a relatively narrow neck, contrasting with the broader connection seen in many cynodonts. The external ramus plays a prominent part in the formation of the zygomatic arch, covering much of its outer surface and, at the posterior end, forming its entire thickness. Anteriorly, it ends in a slender external tongue not far behind the base of the postorbital bar. A short distance back of this point, it reaches the upper margin and retains this position for the length of the arch; broken specimens show that

the upper portion of this squamosal ramus is received in a deep longitudinal groove in the underlying jugal. The upper margin is distinctly thickened. Posteriorly, as the arch curves downward and inward, the upper external surface of this ramus is somewhat channeled longitudinally, with a mildly concave cross-section. This channel corresponds to the much more marked channel in *Cynognathus* which has been interpreted as an external auditory meatus. At the posterior portion of the arch, the lower margin of the squamosal extends downward over the entire width of the jugal and, extending still further downward, forms a somewhat thickened flange covering the posterior portion of the mandible. There is no indication of any specialized surface for articular contact with the dentary, which lies just internal to this flange.

The occipital ramus of the squamosal forms mainly a thin sheet of bone which occupies the anterolateral surface of the occipital crest. At the upper end of the crest, it covers the posterior end of the parietal, and more distally is obviously applied to the anterior faces of the postparietal and tabular. On the anterior face of the occipital crest, the squamosal is separated from the prootic surface of the otic capsule by an unossified gap, presumably cartilage-filled in life, along the line traversed by the vein mentioned earlier as separating parietal and epipterygoid. Toward the outer (and lower) part of the occipital crest, this unossified line of separation increases in breadth. Present here is the anterior opening of the posttemporal fenestra.

In the region of the junction of its two rami, the squamosal has a complex structure. At the forward curving lower termination of the occipital ramus, its lateral margin turns ventromedially, and buttresses the end of the paroccipital process. This area is somewhat concave in external surface; it is the lower end of the presumed auditory meatus, and hence the margin of the squamosal here, together with the adjacent quadrate and articular, may have afforded support for a tympanum. Anteriorly and laterally to this area, the squamosal is specialized for support of the quadrate. The lower margin of the zygomatic arch at its medial end, adjacent to the flange mentioned earlier, shows the typical pair of notches in which the quadrate (with the quadratojugal) was loosely inserted. On the anterior face of the occipital ramus, a thickened area develops at its outer end; this thickened portion descends anterolaterally to aid in forming a socket, facing ventrally, in which lay the main body of the quadrate.

In posterior view, the occiput is essentially triangular in shape, with the apex dorsally at the point where the sagittal crest bifurcates in formation of the occipital crests, and with a nearly flat base formed by the lower part of the occipital complex, with the stout paroccipital processes extending out nearly directly laterally. The two tall occipital crests diverge at nearly a right angle to extend backward and outward and, curving downward, terminate in the area of the jaw articulation. The point of divergence is situated much farther forward than in most earlier cynodonts. As noted above, the parietals extend some distance down the occipital crests. The anterior surface of the crests is formed by the squamosals; the posterior surface is composed of the postparietal medially and the paired tabulars laterally. The tabulars extend

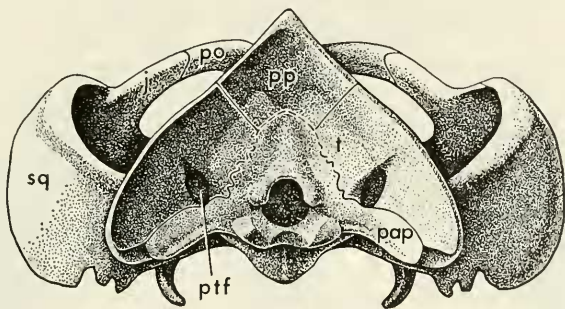


Fig. 4. Occipital view of the skull of *Probelesodon lewisi*.

downward to cover much of the paroccipital processes; the lower parts of these processes, however, are exposed posteriorly. The posterior openings of the posttemporal fenestrae lie above the paroccipitals, within excavations in the ventromedial border of the tabulars. Sutures between the three dermal elements and the occipital complex, which occupies the central area of the occiput, are generally obscure. The occipital elements are fused, without visible sutures; ventrally the occipitals carry the distinctly paired condyles and surround the foramen magnum. On either side of this foramen there are slight swellings which suggest a proatlas articulation.

The anterior end of the palatal surface is formed by the premaxillae. These bones afford insertion for the "incisor" teeth. These lie in the form of a widely opened arch. Close to the midline are the long but very narrow incisive foramina, whose boundaries appear to be entirely formed by the premaxillae; I see no

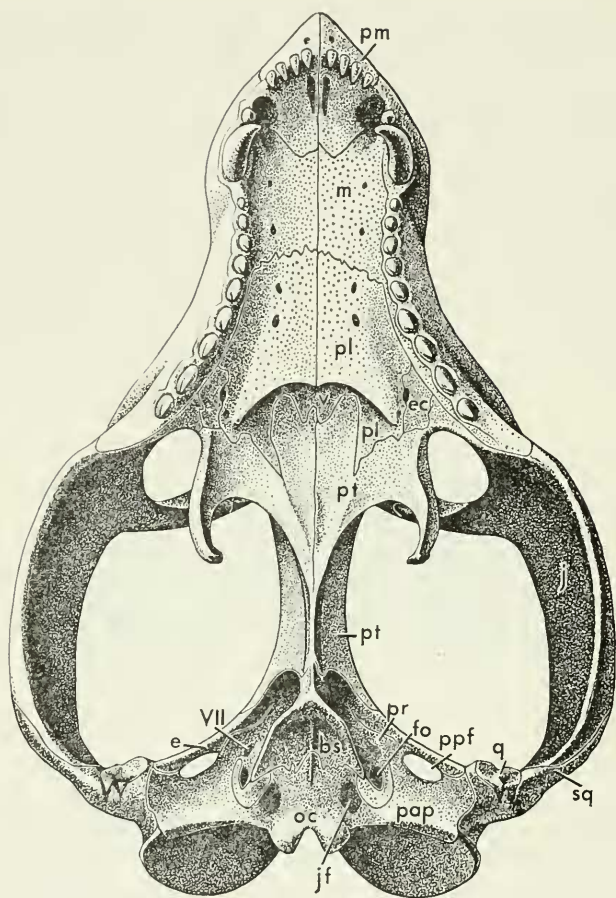


Fig. 5. Palatal view of the skull of *Prohesodon lewisi*.

evidence of the presence of the vomer here. From a point back of the posterior end of the incisive foramina, the sutures between premaxillae and maxillae run laterally, to become lost in the very deep pockets for the reception of the large lower canines. Back of this area stretches the long secondary palate. Approximately half of this structure is formed by the maxillae. On either side of the palate the maxillae form a broad base for the insertion of the cheek tooth series. Anteriorly, the inner margins of the two rows approach one another somewhat more closely than might be

allowed by muzzle width; posteriorly, the tooth rows curve outward in typical cynodont fashion, so that at the back end of the dental series the palatal width is about twice that of its anterior portion. Anteriorly, the tooth bases are close to palatal level; posteriorly, on either side, the inner margin of the maxilla forms a distinct shelf, bearing the line of tooth bases well below the level of the palate. The secondary palate is continued backward to a remarkable degree by the palatines. The palatine portion of the secondary palate is somewhat arched and convex ventrally in transverse section. Posteriorly, the secondary palatal structure does not expand laterally; hence the most lateral portions of the palate here (mainly the ectopterygoid areas) are not involved, and lie at a somewhat higher level than do the palatines. The thin posterior margin of the secondary palate is often broken, but appears to have been somewhat concave in outline as seen from below. Both maxillary and palatine portions of the secondary palate show several pairs of small foramina; a particularly large pair is present at the palatine-ectopterygoid suture.

The secondary palate development here is in strong contrast to that of all other described therapsids (except other, related, chiniquodonts), in which only the most anterior parts of the palatines are involved. In the extent of the secondary palate, the chiniquodonts rival mammals.

Beneath the posterior end of the secondary palate can be seen the posterior end of the vomer. On either side is visible a portion of the palatine forming part of the primary palate; posteriorly, there extends a long finger of the palatine overriding the pterygoid. Lateral to the posterior end of the secondary palate, a small ectopterygoid is persistent, bounded by palatine, maxilla, jugal, and pterygoid. Medial to the distal end of the maxilla, an extension of the jugal runs inward and forward to a contact with ectopterygoid and pterygoid.

There persists a considerable palatal ramus of the pterygoid. Each pterygoid extends forward medial to the palatine "finger" mentioned above, to gain contact with the vomer. Lateral to the palatine there is a second forward extension which gains contact with the ectopterygoid and, briefly, with the jugal. This region includes the area of the primitive pterygoid flange. In many therapsids, notably cynodonts, a ventral process tends to develop which apparently acts as a guide for the lower jaws. In specimens of the present species in which these processes are well preserved, they are more elongate than in any other non-chiniquodont described form.

From the palatine "fingers," ridges run back on either side to converge medially. Lateral to these ridges, the margins of the ventral surfaces of the palatal rami of the pterygoids likewise run back to form ridges parallel to those just described and gradually converging with them. More laterally, the pterygoids are exposed in the floor of the orbits and continue backward as a strip of bone joined dorsally with the epipterygoids. Posteriorly, the pterygoids fuse in the midline and clamp on either side the anterior end of the parasphenoid-basisphenoid complex, forming the median ventral "girder" characteristic of advanced cynodonts, which contrasts with the looser basal connection of palate and braincase present in more primitive synapsids. On either side of the ventral keel of this "girder" is a groove, presumably carrying a blood vessel, bounded externally by a longitudinal ridge. In this ventral region, sutures between pterygoids, epipterygoids, and basicranial structures are not clearly seen. It appears, however, that posteriorly each pterygoid bifurcates, a medial portion sheathing the lateral surface of the parasphenoid-basisphenoid for a short distance and the lateral branch swinging outward to accompany the epipterygoid toward the region of the jaw articulation. A thin plate of bone connecting the two portions forms the floor of the cavity equivalent to the anterior part of the primitive cranioquadrate passage. This passage presumably carried the carotid artery, lateral head vein (if present), and one ramus of nerve VII.

There has been no general agreement as to the relative extent of epipterygoid and pterygoid in the ramus extending toward and to the quadrate region. It is generally believed that the pterygoid is the dominant element here, and that the posterior extent of the epipterygoid is much restricted. The sutural situation in the *Probelesodon* material is obscure, but it seems more reasonable to conclude that here the quadrate ramus is primarily formed by the epipterygoid, and that the backward reach of the pterygoid is limited.

Behind the anterior orbital rim formed by lacrimal and prefrontal, there is a major gap in the side wall of the braincase — a gap filled, of course, in mammals by the orbitosphenoid and extensions of the adjacent dermal elements. Presumably the optic nerve, the eye muscle nerves, and nerve V₁, emerged through this gap. Behind the gap is, as in cynodonts generally, a greatly expanded epipterygoid, lying between parietal and postorbital dorsally and pterygoid ventrally. Its anterior boundary is concave as seen in side view. Posteriorly, it is in contact with the anterior border of the prootic portion of the ear capsule. This region is

not too well preserved in the material available, but there does not seem to be any appreciable epipterygoid overlapping of the prootic, although the suture between the two is an irregular one. Part way down the line of suture is a foramen which is believed to have transmitted nerves V_{2+3} (plus associated blood vessels). Ventrally, an extension of the epipterygoid runs backward and swings outward to the region of the quadrate and squamosal. The epipterygoid forms the anteroventral wall of the pterygo-paroccipital foramen, presumably for venous passage.

Although accommodations for housing the quadrate (+ quadratojugal) in the squamosal are present, as described above, this bone, loosely articulated, tends to drop out when the jaw is disarticulated. It is present in the material only in two cases in which the lower jaws are in place, and in consequence, its structure cannot be completely made out.

Although, as noted, sutural lines are none too clear in the region of the median longitudinal bar formed mainly by the pterygoids, it is obvious that the parasphenoidal rostrum, clamped more anteriorly between the pterygoids, becomes visible ventrally in the posterior part of this bar. The anterior end of the parasphenoid, possibly with an associated sphenethmoid (presphenoid), is surely present internal to the epipterygoids, but I have not attempted to develop this area of the skull. Behind their point of ventral emergence, the conjoined parasphenoid and basisphenoid expand into a roughly triangular area, with raised edges and an essentially flat ventral surface carrying a medial ridge. The anterior portion of this surface is obviously the basisphenoid, covered ventrally by the parasphenoid; the posterior portion is part of the occipital complex, but the suture between the two is generally obscure. On either side of this area is a large jugular foramen, facing ventrally, and presumably carrying nerves IX-XI. I have no certain evidence of hypoglossal foramina. Beyond the lateral rim of the jugular foramen, there is a sharp shift to a laterally facing surface where there is a well-developed fenestra ovalis. I am uncertain as to the sutural relations of the opening. Its anteroventral boundary appears to be formed by the parasphenoid-basisphenoid. In well-preserved specimens, the remainder of the fenestra is bounded by a continuous raised ring of bone, not subdivided, which is separated from the adjacent regions of the otico-occipital complex by distinct grooves. Anterior to the fenestra is the foramen for nerve VII.

Posterolateral to the fenestra ovalis, there stretches the stout paroccipital process of the opisthotic. Laterally it ends bluntly. It

is here buttressed by the squamosal but the tip of the process is unossified; presumably there was some degree of kineticism here. As noted above, the posttemporal fenestra passes forward above the paroccipital process, to emerge anteriorly in a gap between the squamosal and the more anterior, prootic, aspect of the otic capsule. Ventroanteriorly, the paroccipital process thins; at its outer edge it extends downward and forward to reach the posterior end of the quadrate ramus of the epipterygoid. Continuous with the paroccipital process, there is seen on the lateral surface of the braincase (as on the ventral aspect) a forward extension of the otic capsule, the prootic region. Its thin anteroventral margin passes forward and medially to form the upper boundary of the pterygo-paroccipital foramen and then meets, or is covered by, the lateral extension of the parasphenoid. Laterally, the prootic is widely exposed. Dorsally and posteriorly, it is separated from the parietal and squamosal, as noted earlier, by a venous channel; anteriorly, it is in contact with the posterior margin of the broad laterally-facing plate of the epipterygoid; ventrally, it continues in contact with the epipterygoid until the pterygo-paroccipital foramen is reached.

LOWER JAW

(Figs. 6-7)

The lower jaws are present in three specimens. In all three the posterior tip is imperfect. The jaw is of the type characteristic of advanced cynodonts generally. The dentary is dominant, extending almost the entire length of the ramus. It forms nearly all of the strong backward-slanting symphysis. The dentary portion of the lower margin of the ramus is essentially straight. Posteriorly, it terminates at a sharp right angle, as in certain other advanced forms; from this point the ventral boundary of the dentary turns sharply upward and then turns backward with a somewhat thickened lower margin. There is a highly developed ascending ramus, which dorsally curves backward at a moderately sharp angle; thence the boundary curves forward, downward, and backward to terminate just above, and external to, the articular region. It is reasonable to believe that the posterior tip of the dentary was concerned, together with the articular, in jaw articulation.

On the inner surface of the dentary, a sharp ridge extends forward from the posterior tip of the bone, below which the bone is excavated for the reception of posterior elements of the jaw; more

anteriorly, the inner surface is grooved for a narrow meckelian canal which extends from a point just behind the symphysis back to a point where it is covered by the prearticular. Below, and partially covering this meckelian groove, is a thin and narrow splenial, which takes a minor part in the symphysis and extends backward to a point on the posterior margin of the dentary above its angular process.

Of other elements of the "normal" reptilian internal surface of the jaw, there is, in the material, little positive evidence of the coronoid, which was presumably present in life as a thin flake of bone on the inner surface of the dentary in the region of the base

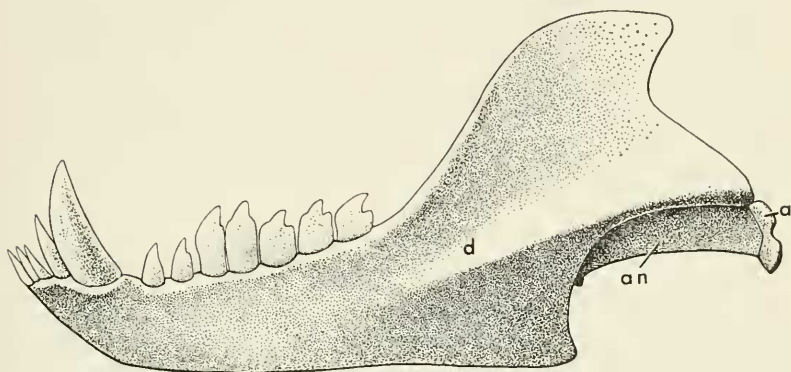


Fig. 6. Lateral view of the lower jaw of *Probelesodon lewisi*.

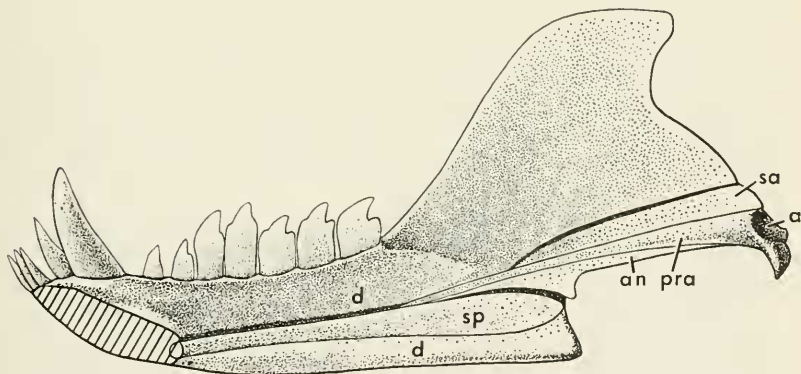


Fig. 7. Medial aspect of the lower jaw of *Probelesodon lewisi*.

of the ascending ramus. Below the assumed position of the coronoid is the slender anterior end of the prearticular, which extends backward, gradually widening, to fuse with the articular. The surangular is completely covered externally by the dentary. In the type, the bone is absent, but its position is obvious because there exists a deep channel for its reception on the inner surface of the dentary; in a second specimen, the bone is present but cannot be completely seen. The angular has a modest external exposure. Internally, the angular is completely covered posteriorly by the prearticular; more anteriorly, there is a narrow exposure of the bone below the prearticular, dwindling to a point anteriorly. Ventrally, just anterior to the point where the dentary covers the bone externally, a small ventral prong is the last remnant of the reflected lamina of the angular, so prominent in the therapsid ancestors. At the posterior end of the jaw, fused to the prearticular, is the articular, essentially an oval structure presenting an articular cup facing posterodorsally, and with a modestly developed retroarticular process.

DENTITION

The dentition is of an orthodox cynodont type. There are four upper incisors in each premaxilla, cylindrical, long, and slender, and set close together in a somewhat arched transverse row; they are slanted strongly backward below the pointed snout. Below, on each side, are three similar incisors directed forward as well as upward. There are well-developed canines both above and below, sharply pointed and slightly recurved; the upper ones are somewhat the stronger. In the holotype, the canines are in process of replacement. Several of the larger specimens have nine upper cheek teeth; the holotype, presumably somewhat immature, has eight, with a ninth erupting posteriorly on one side; an "infantile" specimen has eight. The lower cheek teeth are well seen only in the holotype and in an "infant." In the better preserved of the two rami of the type, there are seven teeth, with, apparently, an eighth developing posteriorly. In the "infant," the lower dentition is not too well preserved, but only six cheek teeth are seen.

The cheek teeth have single roots which are not deep, as witnessed by the fact that in the fossil specimens, they are frequently displaced or lost. (In the related *Belesodon*, for example, all teeth had been lost in the two known specimens, so that one was not even sure whether one was dealing with a carnivore or a gomphodont; in several of the specimens of the Chañares form, a

considerable portion of the cheek teeth had been lost before burial.) The teeth are of a common cynodont type, laterally compressed, sharply pointed, and with a tendency for the development of a fore-and-aft cusp row. As in a number of thrinaxodontids and related chiniquodontids, there is a strong trend for a backward curvature of the major cusp. There is some individual variation, but, in general, in the first two upper teeth — and sometimes in the third as well — there is only a single cusp, curved backward to a slight degree. Back of this, in the upper jaw, there is an increasing development of a posterior accessory cusp, associated with a fore-and-aft lengthening of the tooth. In the only good specimen available of the lower jaw dentition, the development of the posterior cusp is initiated on the second tooth present. In the upper jaw, there tends to be a development of a small anterior cusp, somewhat toward the inner surface. In the one well-preserved lower jaw ramus, an anterior cusp is present on teeth four to six.

I have seen no tendency for the development of accessory "cingulum" cusps, such as might be expected in forms related to mammal ancestry.

THE FAMILY CHINIQUODONTIDAE

In 1956 Watson and I arranged the carnivorous cynodonts in three families in morphologically progressive order — Procynosuchidae, Thrinaxodontidae, Cynognathidae. At that time, we included the then-known chiniquodontids in the Cynognathidae, since they were obviously more advanced than the thrinaxodonts in such characters as the development of a free angle of the dentary. In 1956 Huene erected the family Chiniquodontidae for *Belesodon* and *Chiniquodon*, but gave no definition. These two forms (particularly *Chiniquodon*) were then very poorly known; I have elsewhere (1969) given additional data on these two genera which show that they, plus *Probelesodon*, form a natural group, clearly distinct from the Cynognathidae and that they deserve, as Huene felt, segregation as a separate family of advanced cynodonts. They share with the better known advanced cynodonts such features as the great development of the dentary and corresponding reduction of the other jaw elements. But there are notable differences from the cynognathid condition. For example, they lack the broad posterior connection of zygomatic arch and occipital crest seen in cynognathids, and have retained a more primitive situation here. Again, they lack the longer snout

and proportionately narrow skull of typical cynognathids, and preserve the shorter snout and very broad zygomatic region seen in thrinaxodontids. It is probable that for chiniquodontid ancestry we must look to a descent from thrinaxodontids parallel to that of the cynognathids. *Sinognathus* (Young, 1959), from the early Triassic of China, may be antecedent, although the palate is less developed.

The unique chiniquodontid feature, never attained by known cynognathids or thrinaxodontids, is the remarkable elongation of the secondary palate. This is a very advanced character unrivalled in any other described therapsids, and paralleling the mammalian condition. We have noted above the fact that the dentary is close to, if not actually in contact with, the squamosal; but neither in the present genus nor in the Santa Maria chiniquodonts is there any development of special squamosal-dentary articular surfaces. In described chiniquodonts, as in cynodonts generally, there remains a large unossified area in the braincase wall, to be filled in by orbitosphenoid-presphenoid development before a mammalian condition is reached. *Probelesodon* and its allies may be close to the line of ascent toward mammals, but there is still a considerable distance to go.

CYNODONT ANCESTRY

Above, we discussed the relationship of *Probelesodon* to other cynodonts. It may not be amiss to discuss in addition the unsettled question of the ancestry of the Cynodontia as a whole.

In 1956 Watson and I proposed that the therapsids be grouped in two large suborders, the Theriodontia and Anomodontia — the former term covering the main carnivore groups, such as the Gorgonopsia, Cynodontia, Therocephalia, and Bauriamorpha; the latter term, used in a broad sense, for the herbivores — the herbivorous Dinocephalia, Dromasauria, and Dicynodontia. This proposal appeared eminently reasonable and has, I believe, been rather generally accepted in most regards. However, some years ago (1961) I pointed out one shift which seemed necessary. It seems certain that the ancestral therapsids, of spenacodont descent, were carnivores, and hence Watson and I included in the Theriodontia the earliest and most primitive carnivorous therapsid group then recognized, the Titanosuchia or carnivorous Dinocephalia. But study shows that nearly all the forms usually included in the Titanosuchia possess the peculiarly "shouldered" anterior teeth found in the herbivorous Dinocephalia. It thus

appears that, with this specialization already developed, the titanosuchians cannot be placed in the Theriodontia as a basal therapsid group but must instead be considered as ancestral anomodonts. Where, then, shall we find truly ancestral therapsids? Such types known to me in 1961 included only *Phthinosuchus* and a few other poorly known forms from the early Middle Permian of Russia. In skull structure, *Phthinosuchus* had attained therapsid status, but barely so, and is in many regards closely comparable to the ancestral sphenacodonts. I therefore erected for this genus and its relatives the suborder Phthinosuchia as a basal therapsid stock potentially ancestral to such theriodont groups as the Therocephalia, Gorgonopsia, and Cynodontia, and ancestral, through the Titanosuchia, to the Anomodontia as well.

At about this time Boonstra, whose work has been concentrated in great measure on the reptiles of the Tapinocephalus Zone of South Africa, visited Moscow, familiarized himself with the Middle Permian faunas of Russia, and, on his return home, published (1963) an excellent paper on the early phylogeny of therapsids. Although my work of 1961 was not known to him when he wrote, he had come to very much the same conclusions that I had as regards the interrelationships of early therapsids. He recognized the truly primitive position of *Phthinosuchus* and its relatives, and erected a separate basal group for them. His attention, however, was concentrated not so much on *Phthinosuchus* as on *Eotitanosuchus* (Chudinov, 1960), description of which was not yet available when my 1961 paper was prepared, and he hence used the term *Eotitanosuchia* rather than *Phthinosuchia*.

It seems certain, then, that the Cynodontia are of ultimate phthinosuchian (or eotitanosuchian) derivation. But were they directly derived, or is their descent to be traced through one or another of the familiar theriodont groups? In earlier decades, the Gorgonopsia were rather generally thought to be cynodont ancestors. Such ancestry was long favored by Watson (1920, 1951). In a number of regards, the gorgonopsians represent a primitive morphological stage antecedent to that of the cynodonts (and, as a minor point, are the only therapsid group apart from the cynodonts in which the primitive 2.3.4.5.3 phalangeal formula is known to have been retained). But there are few indications among gorgonopsians of any trend toward a cynodont condition; the gorgonopsians seem to have been, so to speak, "frozen" in a primitive theriodont morphological pattern, and, in addition, universally retain such gorgonopsian "trademarks" as the preparietal bone and a reduced cheek tooth series.

If the gorgonopsians are excluded, where can we turn? In recent decades the Therocephalia, or rather that advanced series of therocephalians termed the "scaloposauroids" (which Watson and I preferred to group with their Triassic descendants, the Bauriamorpha), have been favored as cynodont ancestors. The scaloposauroids show various advanced characters. The skull is lightly built, there is a trend toward a secondary palate, the dentary is well developed, and so on. These trends lead toward the advanced condition seen in *Bauria*; but, it has been suggested, may there not have been a second advanced line leading to the cynodonts? To be sure, most scaloposauroids tend to be long-snouted forms with a long tooth row, with, in general, little differentiation of canines, and with the characteristic therocephalian-bauriamorphan "trademark" of large palatal vacuities. However, reversal in such features might have occurred and if transitional forms were to be found, belief in a scaloposauroid ancestry of the cynodonts would attain credibility.

Broom, although early disposed to a gorgonopsian ancestry, later (1938) inclined toward a therocephalian origin. Brink has been a recent major advocate of cynodont descent from therocephalians, specifically the scaloposauroids (Brink, 1950, 1951).¹ Since Brink is the only writer who has attempted to give broad consideration to the theory of therocephalian ancestry of cynodonts, his arguments deserve careful consideration.

Brink's attention was attracted to some small skulls named *Silphedestes* and *Silphedocynodon*, which are in general scaloposaurid in type, but in which postorbital and zygomatic arches are absent. Whether this absence in the skulls as preserved is due to their absence in life or to post-mortem damage is not certain. The presumed absence of arches has, of course, no bearing on possible cynodont relationships, since these arches (slender in scaloposaurids) are highly developed in cynodonts. Brink (1951: 340) considered that *Silphedestes* (as well as *Silphedocynodon*) was "truly a cynodontid therocephalian, to be more cynodont than therocephalian and that it should be grouped rather under the Cynodontia than under the Therocephalia."

¹ Unlike Watson and myself, Brink considers the scaloposaurs to pertain to the Therocephalia proper rather than to the Bauriamorpha. In this section I have followed him in using "scaloposaur" and "therocephalian" interchangeably for the presumed scaloposaurid ancestors of the cynodonts.

In the papers cited above, Brink failed to give specific reasons for assuming the relationship of cynodonts to these forms (or to scaloposauroids in general). A further specimen, which Brink believed strongly confirmed his belief in the scaloposauroid origin of the cynodonts, was a small skull from the Cistecephalus Zone, which he prepared by the grinding method and reconstructed, and named *Scalopocynodon* (Brink, 1961). It had been damaged posteriorly before burial. Here, as in the silphedestids, zygomatic and postorbital arches are absent, but again, whether this is a natural condition or is due to pre-burial damage is uncertain. The animal is definitely and clearly a cynodont, as Brink agrees, although a cynodont of a primitive sort. It is closely comparable to the procynosuchid cynodonts and differs markedly from scaloposauroids in numerous regards, such as the secondary palate, the dentition with cusped "molars" and highly developed canines, broad alisphenoids, absence of the large palatal fenestrae of scaloposauroids, a cynodont double condyle, and so forth.

On the other hand, Brink lists 17 features which he believes to indicate the relationship of *Scalopocynodon* to the Therocephalia. I shall consider these 17 points in some detail, using Brink's numeration.

Several points may be immediately ruled out. The absence of postorbital and zygomatic arches (2, 3) and the "feeble structure" of the posterior ends of the squamosals (11), if "natural," are suggestive of scaloposauroids, particularly the supposedly archless silphedestids. However, this has nothing to do with cynodonts, in which stout arches are universally present. Cited as a potential scaloposauroid character is the possible entrance of the frontals into the orbital margin (17); however, conditions here are uncertain.

Cited as further evidence for scaloposauroid relationships are various primitive features lost or modified in typical cynodonts but retained in therocephalians and bauriamorphs. These include:

(1, 5, 7). The presence of an interpterygoid vacuity and the consequent similarity of the pterygoids of the specimen to those of therocephalians (p. 144). No interpterygoid vacuity is present in advanced cynodonts, where pterygoids are firmly fused to the basicranial axis; such vacuities are present, however, not merely in scaloposauroids but in all primitive therapsids. The contrast of the parasphenoidal keel and rostrum to those of cynodonts is, of course, due to the fact that the parasphenoid-basisphenoid is, primitively, still free from the pterygoids, rather than fused into the basicranial bar.

(4). In contrast to cynodonts, and like scaloposauroids, the pterygoids are tooth-bearing. This is merely a primitive character, retained in titanosuchians and gorgonopsians as well as therocephalians.

(6). "The transverse bones contribute rather substantially to the pterygoid processes." This is a general primitive therapsid feature. The area of the "transverse" (ectopterygoid) in the specimen being considered is about the same as in, for example, the titanosuchian *Titanophoneus* and the gorgonopsian *Sauroctonus* (Romer, 1961, fig. 11).

(9). The posterior face of the skull had undergone damage before burial and is not figured by Brink. He states, however, that it is therocephalian-like in the shallowness of the occiput and in the fact that the occipital crests are low and not very sharp. This, however, is a generally primitive character; the impression I get from his description is that of, for example, Efremov's figure (1954, fig. 51) of *Phthinosuchus*.

(12). "The parietal region is not sharply crested." This is merely a primitive feature (cf. for example, *Phthinosuchus* [Efremov, fig. 49]).

(13). "The pineal is situated far back." It does not appear to be particularly far back, but a posterior position is a primitive synapsid feature (cf. *Phthinosuchus*, Efremov, fig. 49).

(15, 16). The prefrontals extend well forward and laterally, preventing a lacrimal-nasal contact. Such a contact, seen in cynodonts, is unique among theriodonts; its absence is primitive, not an exclusive therocephalian feature.

Apart from this series of primitive characters retained in *Scalopocynodon* as well as in scaloposauroids, there are three further points mentioned by Brink as supporting therocephalian relationship which are of dubious importance. (8). The sella turcica is shallow in *Scalopocynodon*, and where known in cynodonts is better developed. However, this region is known in but few therapsids, and the significance of variance here is obscure.

(10). One paroccipital process is preserved in Brink's skull; he states that it is shorter and slenderer than that of cynodonts. It appears to be rather shorter proportionately than in cynognathids, but it does not appear to differ notably from the paroccipital process in other cynodonts for which I have available material or illustrations.

(14). Brink agrees that the alisphenoid (epipterygoid) is as broadly developed as in typical cynodonts but without as much overlap of the prootic, and further, the bone is not as high as is

proper in cynodonts. However, the difference in prootic overlap does not appear great, and I see no appreciable difference in alisphenoid height between *Scalopocynodon* and typical cynodonts.

To sum up, such a primitive cynodont as *Scalopocynodon* shows a number of archaic therapsid characters also retained in scaloposauroids. But I fail to see that *Scalopocynodon* furnishes the slightest evidence that scaloposauroids have anything to do with cynodont origins. I find it difficult to believe that long-snouted scaloposaurs with a nearly homodont dentition, large palatal vacuities and, as far as known, a reduced phalangeal formula of 2.3.3.3.3, should rapidly reverse their evolutionary trends, re-acquire stout canines, close their palatal vacuities,¹ re-acquire lost phalanges, and rather abruptly take on various other cynodont characters. It is much more reasonable to believe that the cynodonts evolved directly from primitive therapsids of the *Phthinosuchus-Eotitanosuchus* type without any close affiliation with other theriodont groups. The only argument against such a belief is the negative one that no pre-cynodonts are known from the Tapinocephalus and Endothiodon zones. Possibly the ancestral forms were rare or possibly they were absent from the Karroo before Cistecephalous Zone times — at which time we know that communications between South Africa and Eurasia were open, and that primitive cynodonts were already present in the pre-Ural region of Russia.

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¹ Whaitsiids, it is true, are forms which have lost the palatal fenestrae typical of therocephalians; note, however, that they retain the typical therocephalian ectopterygoid extending back along the pterygoid flange in the same position it occupied when the fenestra was present.

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